



Late-Holocene vegetation dynamics in response to a changing climate and anthropogenic influences – Insights from stratigraphic records and subfossil trees from southeast Lithuania

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ABSTRACT

To increase our understanding of long-term climate dynamics and its effects on different ecosystems, palaeoclimatic and long-term botanical reconstructions need to be improved, in particular in underutilized geographical regions. In this study, vegetation, (hydro)climate, and land-use changes were documented at two southeast Lithuanian peatland complexes – Čepkeliai and Rieznyčia – for the Late-Holocene period. The documentation was based on a combination of pollen, plant macrofossils, peat stratigraphic records, and subfossil trees. Our results cover the last two millennia and reveal the existence of moist conditions in Southern Lithuania between 300 and 500 CE and from 950 to 1850 CE. Conversely, changes towards warmer and/or dryer conditions have been recorded in 100, 600, and 750 CE, and since the 1850s. Significant differences with other Baltic proxies prevent deriving a complete and precise long-term reconstruction of past hydroclimatic variability at the regional scale. Yet, our results provide an important cornerstone for an improved understanding of regional climate change, i.e. in a region for which only (i) few detailed palaeobotanical studies exist and which has, in addition, been considered as (ii) an ecologically sensitive region at the interface between the temperate and boreal bioclimatic zones.

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1. Introduction

Over the last decades the development of proxy records and improvement of dating techniques permitted assessment of long-term climate reconstruction and a better documentation of responses of ecosystems to environmental forcing at the global scale (Wanner et al., 2008; Marcott et al., 2013). Despite these advances, additional efforts are still critically needed, at the regional scale, to

document past climatic variability and ecosystem dynamics from paleoenvironmental archives. In this regard, peatland regions from the Southeast Baltics – located at the interface between the temperate and boreal vegetation zones (BACC Author Team, 2014; Edvardsson et al., 2016a) and influenced by both western oceanic and eastern continental air masses (Gaika et al., 2017) – offer a substantial, yet underexploited potential for the documentation of Late-Holocene hydroclimatic variability.

To date, climatic variations during the Holocene have been documented mostly with pollen-based studies in the Northern Baltic region (Seppä and Poska, 2004; Heikkilä and Seppä, 2010). Late-glacial climatic reversals have been assessed from pollen and chironomid records in the Eastern Baltics and Belarus (Veski et al.,

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2015) and from plant macrofossils and testate amoebae in NE Poland (Gaika et al., 2017). In these regions, the climatic and anthropogenic signals related to e.g. drainage, fires, deforestation, and deposition of nitrogen in peatlands or adjacent regions (Hughes et al., 2008; Gaika et al., 2017) remain, however, difficult to disentangle. In Lithuania, previous studies covering the Late-Holocene remain scarce and have been developed mostly locally and in the framework of archaeological investigations (Stancikaitė et al., 2006, 2009, 2013).

In this study, we combine newly-developed peat stratigraphic records and tree-ring series from subfossil peatland trees to document the vegetation history, climatic dynamics, and land-use changes in Lithuania over the Common Era (CE). In the framework of this multiproxy approach, (i) pollen records with (multi) decadal resolution are used to derive information on local to regional vegetation changes (Huntley and Birks, 1983; Lindbladh et al., 2013). They are complemented by (ii) plant macrofossil analyses that reflect primarily local vegetation dynamics and thereby offer higher taxonomic precision (Dudová et al., 2013). In addition, (iii) tree-ring width and tree replication series from subfossil peatland trees were used to compute annually-resolved information on (hydro)climatic variability (Edvardsson et al., 2016b).

2. Material and methods

2.1. Site descriptions

Peat stratigraphic sequences were extracted from the Čepkeliai wetland complex (54°00'N; 24°30'E; Figs. 1 and 2a, 5858 ha of raised bogs), the largest wetland complex in Lithuania. By contrast to many areas where the natural dynamics of wetland and peatland ecosystems have been profoundly modified by anthropogenic activities, the Čepkeliai wetland has remained a well-preserved, natural complex which makes it of particular interest for research. The wetland complex is located along the marginal zone reached by the Late Weichselian ice sheet (Bitinas, 2012). The entire area is thus underlain by glaciolinnic layers of silty and clayey sands deposited during the onset of the last deglaciation when

meltwater was drained along the ice sheet and when outwash plains were developed (Blažauskas et al., 2007). The landscape is therefore composed of water-filled depressions in which deposition of limnic, biogenic, and minerogenic material has occurred during the Holocene (Stancikaitė et al., 2002; Blažauskas et al., 2007). At present, the wetland complex consists of lowland sedge bogs, black alder swamps, dry *Cladinoso-callunosa* forests, bog islands and lakes. The surface of the wetland is slightly undulating (128.5–134.4 m a.s.l.) and average depth of the organic layers is about 2.3 m, but can locally reach 16.5 m in depth. The region north of the wetland complex is dominated by Lateglacial sand dunes which are mostly forested with pines (Molodkov and Bitinas, 2006).

Subfossil trees were sampled at the Rieznyčia raised-bog complex located about 53 km northwards from Čepkeliai (54°29'N; 24°32'E, 137 m a.s.l., 229 ha, Figs. 1 and 2b). Due to extensive peat mining activities, numerous tree stumps and trunks can be found in deposits adjacent to the Rieznyčia bog and at the present day peat surface.

The region surrounding the study sites belongs to the boreo-nemoral vegetation zone, which is dominated by Scots pine (*Pinus sylvestris* L.), spruce (*Picea abies* (L.) Karst.), and birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth.) (Natkevičaitė-Ivanauskienė, 1983). According to data series from the Varėna weather station, located about 27 km north of the Čepkeliai wetland complex and managed by the Lithuanian Hydrometeorological Survey, the average annual air temperature in southern Lithuania is 6.2 °C, with mean January temperatures of −5.4 °C, and mean July temperatures at approximately 17.7 °C. The mean summer temperature is thereby about 0.5–1.0 °C above the average of Lithuania. Average precipitation is 673 mm yr^{−1}. Moreover, the largest variations of daily temperature are usually recorded for this region in Lithuania and the snow cover often lasts for about 75–80 days yr^{−1}.

2.2. Collection and preparation of peat sequences

For the palaeobotanical analysis, stratigraphic sequences were extracted from the Čepkeliai peatland complex. The coring site is

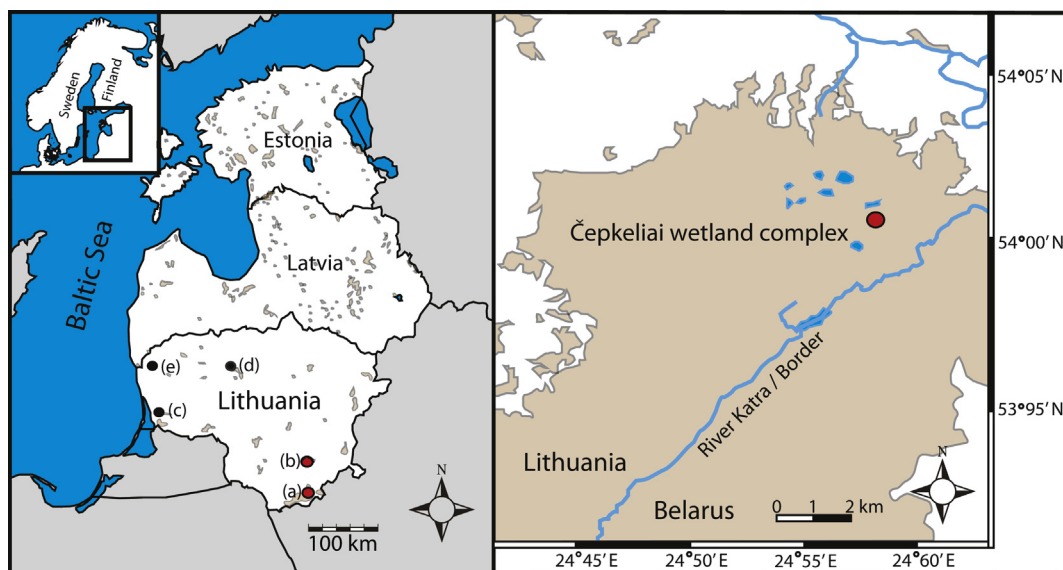


Fig. 1. (a) Overview of the sites described in this study: Red dots show locations of the study sites used: (a) Čepkeliai and (b) Rieznyčia. Black dots show peatlands discussed in the paper, namely (c) Aukštumala, (d) Rekyva, and (e) Užpelkių Tyrelis bog (Pukienė, 1997). Large peatland complexes are shown in brown. (b) The Čepkeliai wetland complex. Wetland and peatland areas are highlighted in brown whereas forested mineral soil areas are shown in white. The red dot shows the coring point. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

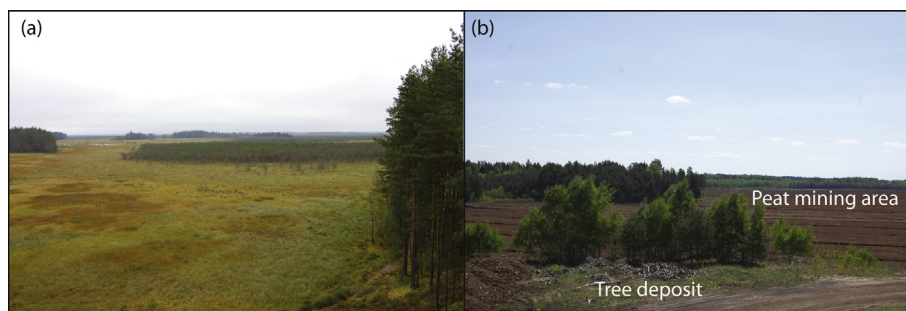


Fig. 2. (a) The analysed peat sequences were obtained from Čepkeliai, the largest wetland complex in Lithuania. (b) Subfossil trees were recovered from deposits and the peat mining area at the Riežnyčia peatland.

located at 131 m a.s.l. in the south-eastern part of the wetland complex (Fig. 1c), and characterized by typical raised bog vegetation. Both birch and pine trees are present in the vicinity of the coring point, and the surface is mainly composed of *Sphagnetum magellanicum*, *Ledo-Pinetum* and *Caricetum limosae* communities (Grigaitė, 1993). Overlapping parallel sediment cores containing biogenic and limnic sediments covering the interval 0–1650 cm were obtained using a Russian peat corer. As a result of non-cohesive material, some mixtures have been observed in the top meter of the peat. As a consequence, analyses focused on the Late-Holocene sequence represented by material from depths between 100 and 204 cm. For information on the Early and Mid-Holocene sequence (depth > 200 cm), we refer to Stančikaitė et al. (2017). At the laboratory, the cores were described in terms of colour, lithological boundaries, and other visible features. Loss-on-ignition (LOI) and magnetic susceptibility were measured for 17 (100–201 cm interval) and 101 (0–204 cm interval) samples, respectively. For pollen analysis, the 100–204 cm interval of the core was sub-sampled at 2-cm resolution. Moreover, samples were taken at intervals of 4 cm for the plant macrofossil survey and for radiocarbon dating (^{14}C).

2.3. Pollen analysis

In total, 27 collected sub-samples (2 cm^3) were prepared following standard chemical procedure (Erdtman, 1936; Grichiuk, 1940) that includes a treatment with a heavy liquid ($\text{CdI}_2 + \text{KI}$). To calculate pollen concentration, a known number of *Lycopodium* spores were added (Stockmarr, 1971). Identification of specimens followed Moore et al. (1991) and at least 500 terrestrial pollen grains were counted to the lowest possible taxonomic level at each sample. Pollen assemblages were calculated as percentages of arboreal (ΣAP) and non-arboreal (ΣNAP) pollen. Pollen diagrams were produced using the programs TILIA and TILIA-GRAPH (Grimm, 1990, 1992). For the calculation, both aquatic taxa and spores were excluded from the sums. Local assemblage zones were determined through stratigraphically constrained cluster analysis (CONISS) (Grimm, 1987) applied to both pollen and macrofossil diagrams.

2.4. Plant macrofossil survey

Macrofossil analyses were carried out on 27 subsamples (30 cm^3) covering 4 cm intervals from the stratigraphic record from Čepkeliai. Following the wet sieving procedure (using screens with mesh sizes of 0.2 and 0.5 mm), remains of plant macrofossils such as fruits, seeds, epidermis, leaves, and scales were extracted from the sediments and analysed using a microscope at a magnification of 20–60 \times . The reference collections available from Grigas (1986),

Berggren (1969, 1981), and Cappers et al. (2006) were used for the identification of specimens; the botanical nomenclature follows Gudžinskas (1999). Results are given in absolute values except for the cumulative diagram (trees/wetland, plants/other/indeterminate), in which frequencies of each taxon were calculated as percentages of the total sum.

2.5. Loss-on-ignition and magnetic susceptibility

Loss-on-ignition (LOI) was determined for the 100–205 cm sequence of the Čepkeliai core following a standard procedure that requires an incineration of the samples at 550°C for 4 h. The core was sampled in 2-cm intervals, but as limited variations were expected in the poorly decomposed peat forming in the upper part of the sequences, analyses of every third sample was considered to be sufficient to capture environmental changes. The information obtained from LOI analyses are presented as percentages of overall weight. Magnetic susceptibility was measured using the MFK1-B kappa bridge (AGICO) at the Palaeomagnetic Laboratory of the Institute of Geology and Geography, Nature Research Centre in Vilnius. The magnetic susceptibility was calculated according to the weight of the sample and expressed as $\text{m}^3\text{ kg}^{-1}$ unit using the SAFYR software (Jelínek, 1977).

2.6. Tree-ring records

During fieldwork campaigns in 2013 and 2014, cross-sections from 104 subfossil pine trees were collected with a chainsaw. In total, 76 cross-sections were sampled from wood deposits, whereas the remaining 28 trees were found *in situ*. The wood samples were dried and sanded with gradually finer sandpaper to enhance the appearance of ring borders and cell structures. Tree-ring width (TRW) series of individual radii were created based on measurement of annual rings using a LINTAB measuring device connected to a stereomicroscope and a computer using the TSAPWin software (Rinn, 2003). To detect wedging rings and possible measuring errors, at least two radii were measured for each sample. Conventional cross-dating based on statistical and visual comparisons between TRW series (Fritts, 1976; Cook and Kairiukstis, 1990) was used, at first for development of averaged TRW series, and thereafter for the development of site TRW chronologies. The quality of the cross-dating, measurements, and the TRW chronologies were evaluated using the COFECHA software (Holmes, 1983). To minimise the influence of non-climatic variations and trends, for example related to tree age and geometry, the TRW series were standardized and transformed into dimensionless TRW indices (Fritts, 1976; Cook and Kairiukstis, 1990). As many trees showed narrow rings during both establishing and terminating years, a flexible standardization method based on Friedman's variable span

smoother (Friedman, 1984) was applied. In order to assess the reliability of the TRW chronologies, the expressed population signal (EPS) was calculated and the limit at which the chronologies were considered as reliable and well replicated was set to the commonly applied limit of $\text{EPS} \geq 0.85$ (Wigley et al., 1984). Both standardization and calculation of the EPS value were made using the software ARSTAN_41d (Cook and Krusic, 2006). Thereafter, tree-replication records were developed for detection of germination and die-off events (Leuschner et al., 2002). Tree replication records were developed based on year-by-year counting of overlapping trees used in the TRW chronologies.

2.7. Radiocarbon dating

In total, five (three from 100 to 205 sequence, one above and one below) peat and six wood samples were radiocarbon (^{14}C) dated. They enabled the development of stratigraphic age-depth models based on accumulation rates for the peat and the dating of the subfossil wood material. The samples were analysed at the Laboratory of Nuclear Geophysics and Radioecology at the Nature Research Centre in Lithuania. Calibration of the ^{14}C measurements to calendar ages (BCE/CE) were performed by applying Bayesian sequence modelling by using the OxCal v4.2 software (Bronk Ramsey, 2001, 2008). For peat samples with known stratigraphic context and for wood samples with known relative ages, *P* or *D_Sequence* analysis (Bronk Ramsey et al., 2001) was used to improve the accuracy and to tie the radiocarbon dates to narrower intervals on the IntCal13 radiocarbon calibration dataset (Reimer et al., 2013). These methods are based on the non-linear relationship between radiocarbon and calendar ages, and were applied by fitting sequences of at least two radiocarbon dates with known age or depth intervals between the radiocarbon calibration curve. At least two wood samples with known number of annual growth rings in between were therefore extracted from each TRW chronology. Ages given are the calculated mean values (μ) from *R_Date*, *P_Sequence* or *D_Sequence* probability curves. The presented radiocarbon data are reported with 2 sigma errors.

3. Results

3.1. Radiocarbon dating

Results from the radiocarbon dating of the peat and wood samples are presented in Tables 1 and 2, respectively. The samples Vs-2635, Vs-2713, and Vs-2712, sampled from the 100–205 cm peat sequence, were dated to 115 BCE–620 CE, 580–900 CE and 765–1030 CE, respectively. In addition, Vs-2714 (250–254 cm, 1265–970 BCE) and Vs-2720 (82–84 cm, 1270–1320 CE) were used to complement the stratigraphic age-depth model (Fig. 3) and to estimate peat accumulation rates. Wood sequences RILS109 (55 rings), RILS033 (200 rings) and RILS020 (165 rings) were dated to the 2nd/3rd, 8th/9th and 7th century, respectively (Table 2). They were used to approximate the age of the floating TRW chronologies

from Rieznyčia (Table 3).

3.2. Lithostratigraphy and age control of the sediment sequence

The studied peat sequence is dominated by organic material with maximum values reaching up to 96% (Fig. 3). Minor deviations in the LOI curve and the magnetic susceptibility measurements suggest a stable sedimentation environment during the development of the sequence. The radiocarbon dates appear in stratigraphic order, which suggests an absence of old-carbon phenomenon, sedimentation hiatus, or any large deviations from uniform accumulation rate in the sequence.

3.3. Regional vegetation record (pollen data)

Based on the CONISS cluster analysis, four statistically significant local pollen assemblage zones (LPZ) were differentiated, two of them being subdivided into sub-zones (Fig. 4). The abundance of arboreal pollen (AP) recorded in \check{C}_{P-1} (205–199 cm) is based on *Betula* (up to 26.9%) and *Pinus* pollens (46.0–56.1%), while other trees (including *Alnus*) are represented sporadically. Poaceae (4.4%), Cyperaceae (3.2%), and *Artemisia* (0.8%) are the most frequent non-arboreal taxa (NAP). Ongoing predominance of AP is recorded in \check{C}_{P-2} (199–146 cm) dominated by *Pinus-Picea* pollens. In \check{C}_{P-2a} (199–180 cm), *Pinus* represents up to 81.8% whereas the assemblage contains 9.3% of *Picea*. At the same time, *Alnus* and *Betula* percentages decreased, and the number of NAP pollen became negligible. Poaceae and Cyperaceae are presented continuously (1.8%–4.0%), but the percentages of other taxa and the number of *Sphagnum* spores decreased in this cluster.

Although representation of broad-leaved taxa i.e. *Quercus* (up to 1.1%) and *Tilia* (0.5%), is higher in the \check{C}_{P-2b} zone (180–146 cm), pollen grains from *Pinus* (up to 85.8%) and spruce still predominated the spectra. Scattered representation of *Carpinus* and *Fagus* suggests the regional origin of the mentioned taxa. The total amount of NAP remains negligible (less than 1.7%) but the sporadic occurrence of Anthropogenic Pollen Indicators (API) – such as *Plantago*, *Scleranthus*, *Urtica*, ruderals, including *Artemisia* with *Chenopodium*, and heliophilous herbaceous taxa like *Taraxacum* and Caryophyllaceae – evidence occupation phases of the peatland.

A significant change in the vegetation composition is observed at the onset of \check{C}_{P-3} (146–111 cm). *Betula* and *Alnus* (up to 7.2%) recovered during this time, whereas *Pinus* (60–80%) and *Picea* (4.9%) decreased in the pollen spectra within \check{C}_{P-3a} (146–130 cm). At the same time, an increasing presence of deciduous taxa is revealed by the continuous representation of *Quercus* pollens accompanied by a higher frequency of *Tilia*, *Ulmus* and *Carpinus*. Higher percentages of NAP, especially Poaceae and Cyperaceae (up to 1.9% and 3.4%), are also recorded. In the \check{C}_{P-3a} zone, increasing representation of API, including continuous representation of *Artemisia* and higher frequency of *Plantago*, coincide with changes in extra-local vegetation revealed by *Filipendula* (up to 4.1%) and Ericaceae.

At the onset of \check{C}_{P-3b} (130–111 cm), *Pinus* pollen reincreased in

Table 1
Radiocarbon (^{14}C) data from the Čepkeliai peat sequence.

Lab code	Depth (cm)	Material analysed ^a	Produced benzene (g)	^{14}C -age (yr. BP)	Cal yr. BCE/CE 95.4%
Vs-2720	82–84	TOC	2.60159	680 ± 35	1270–1320 CE (58.4%)
Vs-2712	138–142	TOC	0.68454	1125 ± 70	765–1030 CE (92.3%)
Vs-2713	162–166	TOC	0.41263	1300 ± 90	580–900 CE (92.8%)
Vs-2635	196–200	TOC	0.22048	1765 ± 170	115 BCE–620 CE (94.7%)
Vs-2714	250–254	TOC	1.88567	2915 ± 55	1265–970 BCE (93.0%)

Vs-2720 and Vs-2714 – ^{14}C dates applied for the calculation of age-depth model.

^a TOC – total organic carbon.

Table 2
Radiocarbon dating of wood samples from tree-ring chronologies.

Tree id. no. (used rings)	TRW chronology	¹⁴ C-age (yr. BP)	Cal yr. CE (Un-modelled)	Cal yr. CE (Modelled)
RILS020 (50 ± 5)	RiBC01	1280 ± 40	760 ± 104	696 ± 36
RILS033 (70 ± 5) 39 ^a	RiBC01	1330 ± 35	707 ± 64	735 ± 36
RILS033 (195 ± 5) 125 ^a	RiBC01	1160 ± 35	875 ± 104	860 ± 36
RILS109 (20 ± 5)	RiBC02	1880 ± 30	144 ± 78	104 ± 72
RILS109 (160 ± 5) 140 ^a	RiBC02	1820 ± 25	219 ± 92	244 ± 72
RILS111	RiBC03	1965 ± 30	37 ± 78	–

^a No of annual growth rings between this wood sample and the sample above in the table.

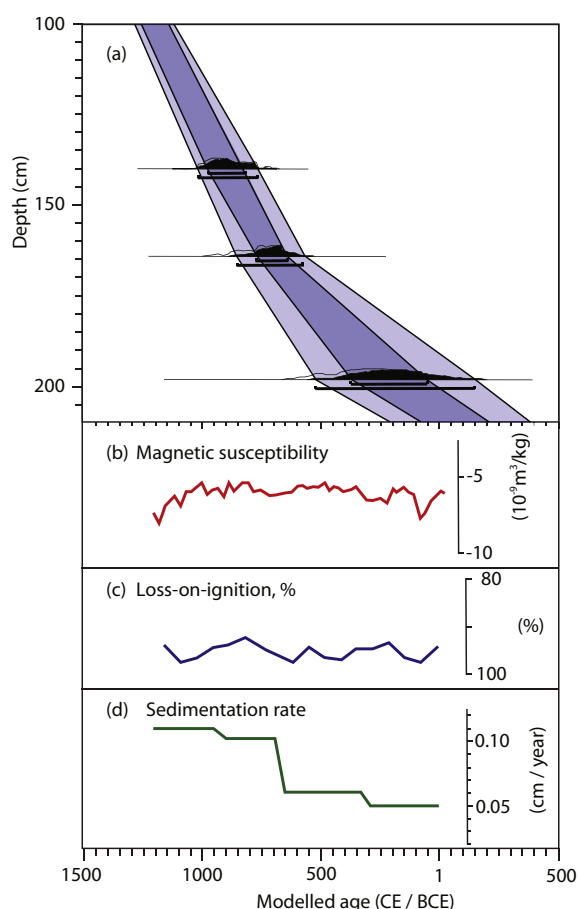


Fig. 3. (a) Age-depth model for the analysed peat sediment sequence from Čepkeliai wetland complex and lithostratigraphical data, namely (b) magnetic susceptibility, (c) loss-on-ignition and (d) sedimentation rate.

the spectra (up to 76.1%) whereas amounts of *Betula* and *Alnus* were lowered. Diversification of anthropogenic pollen indicators (*Plantago*, *Scleranthus*, *Urtica*, *Rumex*, *Chenopodium*, *Taraxacum*) are clearly observed in Č_{P-3b}.

In the uppermost cluster, Č_{P-4} (111–101 cm), the total number of AP pollen is lowered suggesting the opening of forests. The frequencies of *Pinus* and *Picea* dropped to 49.3% and 2.7%, respectively. *Betula* and *Alnus* recovered at the same time, reaching up to 22.1%

and 5.9% of the pollen spectra. The representation of *Quercus* remains continuous whereas other broadleaved taxa are represented only sporadically. Culmination of *Artemisia* is accompanied by the rise of *Chenopodium* and *Plantago* suggesting possible human interferences. Both Cyperaceae (5.5%) and Poaceae (5.3) show high values within this zone.

3.4. Local vegetation pattern (plant macrofossil data)

The plant macrofossil assemblage from Čepkeliai consists of 14 species and genera. Eight of them were identified down to the species level and six indicated as a genus. Once identified, the taxa were grouped according to habitats and divided into trees, wetland plants, and others. The diagram has been sub-divided into four zones with sub-zones within zone Č_{M-3} displaying changes of the macrofossil assemblage (Fig. 5).

In zone Č_{M-1} (210–173 cm), remains of *Betula* sect. *Albae* and *B. pubescens* indicate the establishment of these tree species in the close vicinity of the sampling site. The presence of *Menyanthes trifoliata*, *Oxycoccus*, *Carex* cf. *canescens* and *Scheuchzeria palustris* and the continuous record of *Potentilla* sp. suggest the abundance of these taxa at Čepkeliai. In zone Č_{M-2} (173–144 cm), an increasing taxonomic diversity is recorded. *Betula* sect. *Albae* macrofossils are present throughout the zone. *Menyanthes trifoliata*, *Carex elata* and *Andromeda polifolia* macrofossils are increasingly represented. Only *Potentilla* sp. remains decreased temporarily in number.

The sub-zone Č_{M-3a} (144–124 cm) is characterized by a stronger presence of *Andromeda polifolia* and *Menyanthes trifoliata* associated with a reincrease of *Potentilla* macrofossils. This latter species as well as *Menyanthes trifoliata* and *Carex vesicaria* are replaced with *Carex* sp., *Carex elata*, *Carex paniculata* in Č_{M-3b} (124–112 cm). *Betula* sect. *Albae* macrofossil remain frequent in this sub-zone. Finally, the Č_{M-4} cluster (112–101 cm) is characterized by the synchronous reappearance of *Menyanthes trifoliata*, *Carex vesicaria*, *Scheuchzeria*, and *Oxycoccus*, whereas *Carex elata* progressively disappeared from the spectra.

3.5. Tree-ring data

Two TRW chronologies, 321 (RiBC01) and 216 (RiBC02) years long, respectively, were developed from the pine material collected at Riežnyčia peatland (Tables 2 and 3). The main TRW chronology (RiBC01) was constructed from 62 pine samples and radiocarbon dated to 635–955 ± 36 CE (1314–994 ± 36 cal. BP; Table 3). The replication record shows establishment phases about

Table 3
Basic information about the tree-ring chronologies.

Site/Code	No. trees/Length (yrs.)	Covered period (Cal yr. CE)	Inter-series corr. (r)/Mean TRW (mm)
Riežnyčia/RiBC01	62/321	635–955 ± 36	0.544/0.58
Riežnyčia/RiBC02	9/216	76–291 ± 72	0.562/0.51
Riežnyčia/RiBC03	1/391	35 BCE–355 ± 78	0.000/0.73

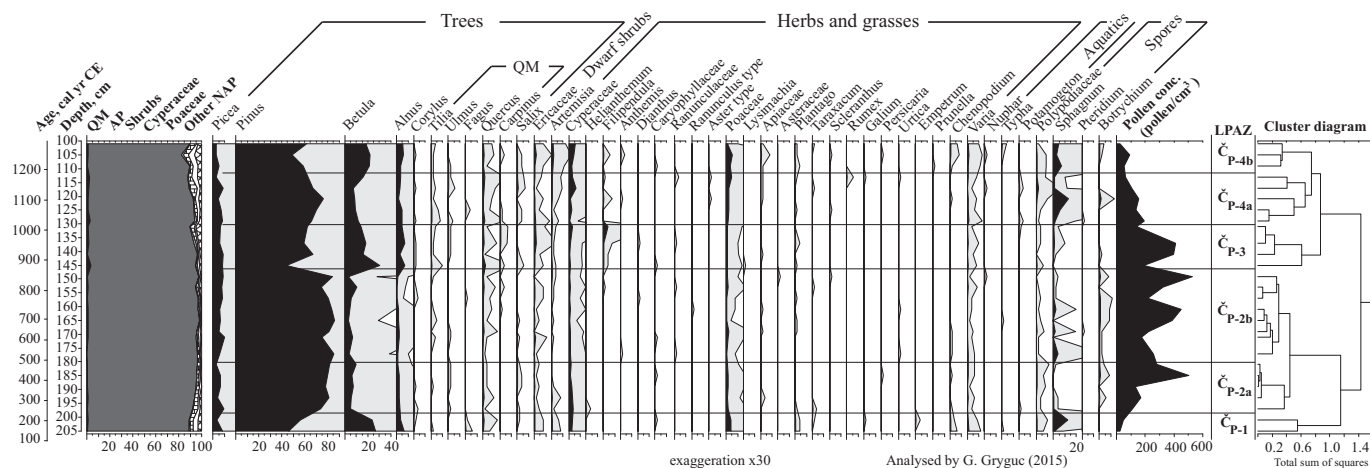


Fig. 4. Pollen percentage diagram from the Čepkeliai wetland complex.

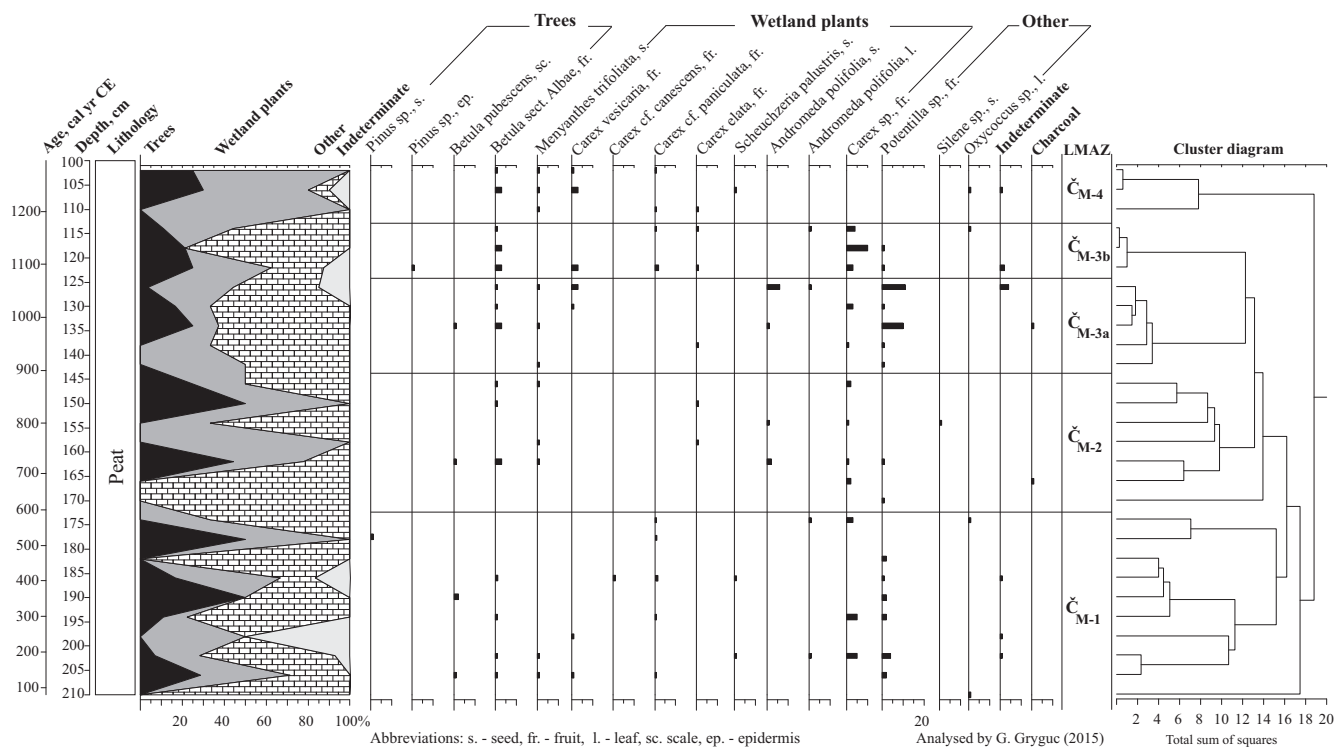


Fig. 5. Plant macrofossil data from the Čepkeliai wetland complex.

650 and 750 CE, followed by a massive dying-off event about 900 CE (Fig. 6). The TRW data show seven extended periods, three years or longer, of depressed tree growth (TRW Indices < -1 SD). The second TRW chronology (RiBC02) was constructed from 9 trees and radiocarbon dated to $76\text{--}291 \pm 72$ CE. In addition to the trees used to develop the two TRW chronologies, a long-lived tree (age >391 yrs) was dated by radiocarbon. This tree (Ri111) lived approximately 35 BCE to 355 CE, and is of contemporary age with nine trees used in the RiBC02-chronology. Despite this synchronicity, significant cross-dating statistics could not be obtained between the samples. The Ri111-sample was therefore interpreted as a tree growing on mineral soil due to the relatively even annual growth and the lack of correlation with the other material from the same site.

4. Discussion

Our multiproxy approach – based on peat, pollen and macrofossil records – enables a differentiation of four periods in the Late-Holocene development of the Čepkeliai wetland complex to evidence environmental and regional (hydro)climatic changes in southeast Lithuania between 100 and 1800 CE. Colonization and dying-off phases detected in the subfossil tree records from the Riežnyčia peatland as well as depressed tree growth in tree-ring series have been used as an independent indicator of (hydro)climatic dynamics in the region. In addition, in order to enable further upscaling, comparisons have been made between our dataset and other long-term palaeobotanical and hydrological reconstructions available for the Baltic region.

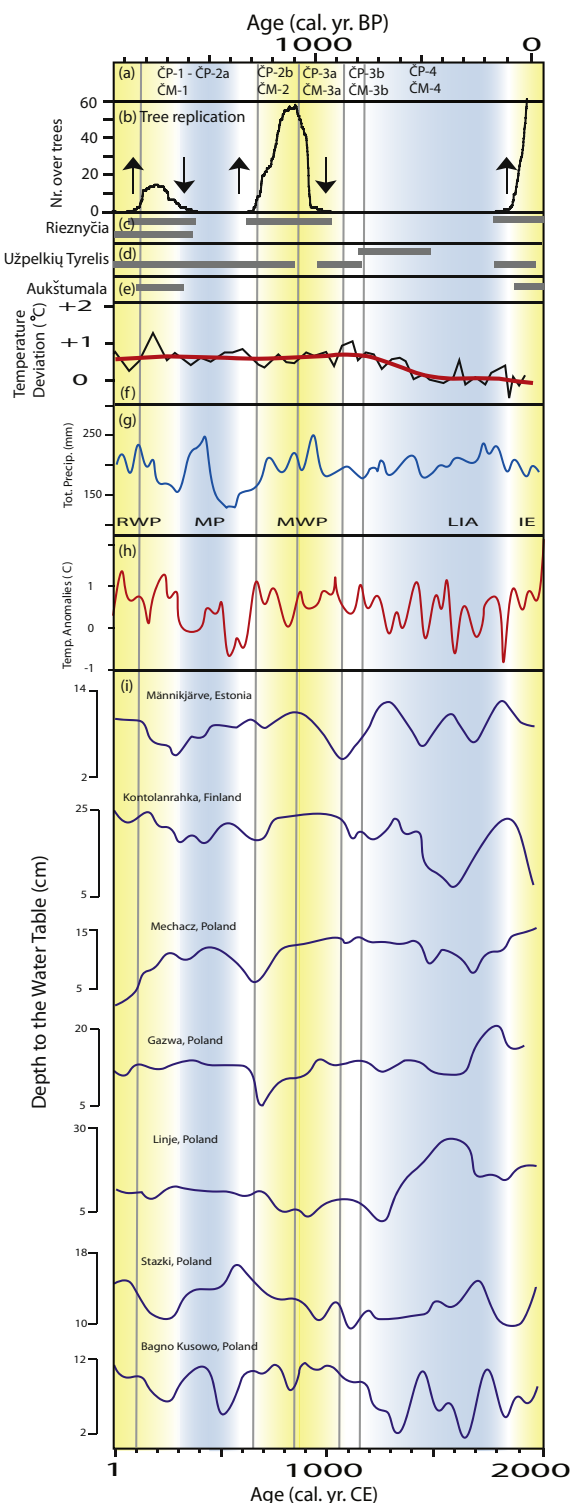


Fig. 6. Summary image showing warm/dry (yellow) and cold/wet (blue) phases with abbreviations for the approximate intervals for historical periods, namely the Roman Warm Period (RWP), the Medieval Period (MP), the Medieval Warm Period (MWP), the Little Ice Age (LIA) and the Industrial Era (IE). (a) The abbreviations and vertical lines show periods identified from the pollen record used in this study. (b) The Rieznycia tree replication record. The grey lines (c–e) show temporal distribution of subfossil peatland trees from (c) Rieznycia, (d) Užpelkių Tyrelis (Pukienė, 1997, 2003), and (e) Aukštumala (Edvardsson et al., 2016a). (f) Temperature reconstruction from Latvia (Heikkilä and Seppä, 2010). (g) Precipitation and (h) temperature reconstruction from W. Europe (Büntgen et al., 2011). (i) Water-table reconstructions from peatlands (Gaika et al., 2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.1. 100–650/600 CE (ČP-1 – ČP-2a, ČM-1)

Our palaeobotanical records suggest a predominance of forest communities in the surroundings of the Čepkeliai wetland complex during the early part of the Common Era (CE), which is typical in the eastern Baltic region for the onset of the first millennium CE (Stančikaitė et al., 2002; Novik et al., 2010; Stivrins et al., 2015). This afforestation could have been related to an increase in temperature noted in the Baltic area at about 100 CE (Seppä and Poska, 2004). From a local perspective, it is likely that pine trees grew in the surroundings of the peatland whereas *Betula*, including *Betula* sect. *Albae* and *Betula pubescens*, highly represented in the pollen diagram, probably grew in the immediate vicinity of the coring point, especially before 230–250 CE. We can also hypothesize that alder colonized the wet habitats situated along the edges of the wetland and can periodically be detected in inundated areas associated with less competition from other tree species (Ellenberg, 1996; Madeja, 2013). *Picea* pollen grains have been noted regionally (Stančikaitė et al., 2002, 2004) with a more limited abundance than observed in our data. This discrepancy suggests an establishment of spruce trees in ecologically suitable areas in the surroundings of the wetland complex. NAP pollens reveals that open habitats were dominated by Poaceae and Cyperaceae. The synchronous occurrence of *Chenopodium* and *Artemisia* about 150–200 CE, as well as meadow plants such as *Plantago* in the spectra suggest high nitrogen-soil levels and probable human activity in/or at the vicinity of the peatland.

The Rieznycia tree-ring records (Fig. 6) indicate relatively dry conditions and tree colonization at the onset of the period. An establishment of pine trees has been recorded at Rieznycia 76 ± 72 CE, pointing to relatively dry peatland surface conditions (Boggie, 1972; Edvardsson et al., 2016b). Synchronous pine establishment has also been recorded at the Aukštumala (Edvardsson et al., 2016a) and Užpelkių Tyrelis peatlands (Pukienė, 1997), which reinforces the hypothesis of regionally warm and dry conditions in the southern Baltic region during the early portion of the discussed period. During the same time, low lake levels have been recorded from southwest Europe (Desprat et al., 2003), south-central Sweden (Harrison and Digerfeldt, 1993) and Poland (Madeja, 2013). The period, sometimes referred to as the Roman Warm Period (RWP), can also be detected in summer temperature reconstruction from Latvia (Heikkilä and Seppä, 2010) as well as Central Europe (Büntgen et al., 2011).

The (hydro)climatic conditions may, however, have shifted towards more humid during the mid-part of the period, which in turn caused the dying-off phase recorded 200–300 CE. This hypothesis is supported by the synchronous dying-off phase recorded at the Aukštumala peatland in western Lithuania (Edvardsson et al., 2016a). Moreover, tree Ri111, interpreted to have been a mineral soil pine (Fig. 6), died at about 355 CE to be buried in peat, which may have been a consequence of increased *Sphagnum* growth at the site following moister conditions. Rising water tables have also been noted in other S/SE Baltic peatlands about 300 CE (Gaika et al., 2013; Lamentowicz et al., 2015).

At Čepkeliai, the percentages of herbaceous taxa sharply decreased after 230/250 CE suggesting changes in the forest structure and the shrinkage of open plots. The increasing percentage of pine pollen contemporaneous with decreasing representation of birch, alder, oak, and spruce further support this hypothesis of an afforestation. In addition, the presence of *Pinus* sp. and *Betula pubescens* macro remains indicate that the peat surface periodically dried strongly and sustainably enough for trees to colonize (Edvardsson et al., 2016b). The plant macrofossil record with *Andromeda polifolia*, *Oxycoccus* sp., *Scheuchzeria palustris* and *Carex* sp. indicates ongoing development of a raised bog

environment despite the apparent existence of low water table conditions. The occurrence of *Carex* cf. *paniculata* even suggests an increasing shallowness of the basin and the formation of a fen with sedges (Gałka et al., 2014). This evolution differs from the regional scheme suggesting a shift toward humid conditions. It may be explained – as observed by Gałka et al. (2017) in the Mechacz Wielki raised bog (Northern Poland, Fig. 6) for the period 250–500 CE – by local conditions such as terrestriation (filling up of the lake) during the first stage of bog development.

4.2. 650/600–850 CE (\check{C}_{P-2b} , \check{C}_{M-2})

Our palaeobotanical records suggest that various types of *Pinus* dominated forest stands coexisted in the surroundings of the Čepkeliai wetland complex between 650/600–850 CE. Oak-pine mixed forests – the existence of which is assumed through the increasing proportion of *Quercus* pollen grains – probably occupied areas with more fertile soils whereas *Picea* potentially persisted in more acidic lowland areas along the water rim of the peatland. Most likely, the plant macrofossils of *Betula pubescens* and *Betula* sect. *Albae* originate from the trees that grew on the peatland or in its closest proximity. At the same time, the disappearance of birch and alder pollens are in line with regional records presented by Stancikaitė et al. (2002).

With respect to NAP, the decay of *Carex vesicaria*, *C. cf. canescens* and *C. cf. paniculata*, as well as increased representation of *Menyanthes trifoliata*, indicate that the water table slightly raised at Čepkeliai. This hypothesis is supported by the appearance of *Typha* pollen, thus indicating shallow water and the development of a littoral zone (Hannon and Gaillard, 1997). Simultaneously, the decreasing frequency of *Potentilla* sp. and the apparition of *Andromeda polifolia*, probably in the driest areas, confirm the continuous formation of a raised-bog environment. This hydro-climatic signal could potentially interfere with anthropogenic activity evidenced by the presence of APIs – such as *Plantago*, *Scleranthus*, *Urtica*, *Chenopodium* and *Taraxacum* – in the pollen spectra. Yet, we assume that human activity remained very limited in the moist terrains surrounding the investigated area.

At Riežnyčia, the initial tree colonization phase recorded about 650 CE, followed by a massive tree establishment stating at around 750 CE (Fig. 6), rather suggests a lowering of the water table. A similar pattern has been observed at the Užpelkių Tyrelis peatland (Pukienė, 1997), indicating a shift towards warmer and/or drier conditions (Edvardsson et al., 2016b) that could be easily related to the Medieval Warm Period recorded in western Europe (Bertland et al., 2002; Tiljander et al., 2003; van der Linden and van Geel, 2006; Lamentowicz et al., 2008). Yet, such an assumption must be considered with caution as (i) no extreme temperature shift was recorded in the reconstruction from the northern Baltics (Heikkilä and Seppä, 2010) and as (ii) the synthesis of water-table fluctuations in Baltic peat bogs, developed by Gałka et al. (2017), points to site-dependant dynamics rather than regional, climatically induced, variations during this period (Fig. 6).

4.3. 850–1050 CE (\check{C}_{P-3a} , \check{C}_{M-3a})

Between 850 and 1050 CE, the palaeobotanical records from Čepkeliai reveal significant changes in the structure of the vegetation. The period is thus characterized by (i) the recovering of birch and alder, (ii) an increasing taxonomic variety of thermophilous tree taxa which has been accompanied by (iii) a simultaneous retreat of pine trees and a decline of spruce. The more noticeable representation of broad-leaved taxa could be explained by increased annual air temperature (Korhola and Weckström, 2000; Seppä et al., 2009) related with the Medieval Climate Anomaly

(MCA, ca. 750–1350 CE) observed at the regional scale (Stivrins et al., 2015). The expansion of *Alnus* and *Betula* pollen grain suggests an increase of shoreline woodlands in the surroundings of Čepkeliai due to a water-table lowering and, in parallel, a higher proportion of *Betula* sect. *Albae* macro-remains originate from the expansion of birch stands on the bog. Contemporary changes recorded in pollen diagrams from Lithuanian lakes show similar drops in water level and extensive development of shoreline habitats (Antanaitis-Jacobs et al., 2002; Heitz-Weniger, 2014).

About 1000 CE, the maximum in *Filipendula* pollen percentage reveals the development of wet meadows in the lakeside areas. Moreover, the increasing representation of Cyperaceae indicates the formation of sedge belts, as the mentioned taxa probably benefited from the assumed lowering of the water table. Subsequently, a complex landscape structure with open vegetation patches characterized by specific vegetation emerged at the study site. The formation of extensive dry habitats is clearly attested by the increasing representation of Ericaceae and the culmination of *Potentilla* sp. In addition, the low representation of aquatic taxa points to a restriction of limnic depositional environments. These evolutions are in line with several records indicating drier surface conditions in peatlands and lowered lake levels across northern and eastern Europe (Lamentowicz et al., 2008; Välranta et al., 2012; Gałka et al., 2014; Stivrins et al., 2015). Such changes could also have resulted from a decrease in annual and summer precipitation (Graham et al., 2010; Kuijpers et al., 2012). At the same time, the complex structure of the environment is attested by *Andromeda polifolia* macrofossils that developed in the remaining plots of the raised bog whereas scattered pollen grains of *Artemisia* and *Plantago* confirm the continuous, albeit limited, human pressure at the site.

The Riežnyčia tree-replication records reveals a dense tree coverage at the onset of the period. The massive dying-off event recorded about 900 CE (Fig. 6), however, indicates that a rapid change towards moister conditions took place centuries before the end of the MWP (~1200 CE). This shift is compatible with warm, but wet summer conditions reconstructed in Western Europe at this period (Büntgen et al., 2011). Yet, overlapping data series from different sites and further (hydro)climatic proxy records from the Baltic region are needed to make sure that the dying-off phase was caused by climatic fluctuations and not by site-related hydrological changes. These observations underline the importance for further and more detailed environmental records from this geographic region.

4.4. 1050–1150 CE (\check{C}_{P-4a} , \check{C}_{M-3b})

Changes recorded in both the plant-macro fossil and pollen diagrams suggest some adjustments in the terrestrial and the limnic vegetation after 1050 CE. The proportion of *Betula* and *Alnus* pollen grains in the spectra decreased. Alder, a typical species at shoreline woodlands (Madeja, 2013), showed the sharpest decrease and almost disappeared from the macrofossil records. On the contrary, the drop of birch is less pronounced and the species remains present in the plant macrofossil record thus confirming its presence at the immediate vicinity of the coring point. These changes in the onshore vegetation may have favoured the aerial transportation of *Pinus* and *Picea* pollen grains, and thereby caused an over-representation of these taxa in the pollen diagram. The surrounding woodlands remain, in any case, dominated by *Pinus* mixed with *Tilia*, *Quercus* and *Picea*.

At the sedimentary basin, palaeobotanical data suggests an extension of the shorelines colonized by wetland plants or aquatics and thereby reveals an increase of the water table. Occurrence of *Typha* and *Potamogeton* pollen grains indicate the formation of

shallow water habitats. In parallel, the culmination of *Sphagnum* and the depletion of wetland taxa such as *Filipendula*, *Potentilla* sp., Ericaceae recorded in both the pollen and plant macrofossil data indicate increasing wetness whereas *Carex vesicaria* and *Carex* sp. formed a sedge belt and *Salix* established on the shores. In line with these results, the absence of peatland trees at Rieznyčia is a further indication of moist conditions (Fig. 6). Similarly, unstable water tables were dated to the 11th century CE in Lake Araiši in Central Latvia (Stivrins et al., 2015). During this period, anthropogenic indicators occurred sporadically. We consider that scattered pollen grains of *Chenopodium*, *Plantago*, and *Scleranthus* recorded in the pollen spectra did most likely result from episodic land use rather than from permanent human settlements at the site, as the known inhabited areas were several kilometres away from the studied area (Stancikaitė et al., 2002).

4.5. Since 1150 CE (\tilde{C}_{P-4b} - \tilde{C}_{M-4})

Since 1150 CE, the pollen data shows an increased proportion of non-arboreal taxa, therefore suggesting a fragmentation of the forest stand. *Artemisia*, Cyperaceae and Poaceae culminate whereas *Plantago* and *Chenopodium* are continuously represented in the pollen spectra. These dynamics are in line with several palaeobotanical studies suggesting a regional change towards a semi-open landscape during this period (Veski et al., 2005; Stancikaitė et al., 2009; Stivrins et al., 2015). Simultaneously, arboreal pollen records indicate an increased occurrence of *Betula* and *Alnus* in the Čepkeliai area, whereas reduced proportions of *Pinus* and *Picea* suggest a reduction of these taxa in the local habitat. Such vegetation changes indicate that, despite the fragmentation, areas with shallow water still persisted in the Čepkeliai region. This hypothesis is further corroborated by the presence of hygrophilous species such as *Carex vesicaria*, *Menyanthes trifoliata*, *Typha* and *Nuphar* in our palaeobotanical records.

Paradoxically, the existence of areas with shallow water may be related to the onset of the Little Ice Age (LIA). Indeed, the LIA is usually associated with changes towards colder and dryer conditions all over Europe (Wanner et al., 2011). These changes should, at least theoretically, be favourable to peatland water-table lowering and tree colonization. Yet, such cold conditions may also have led to limited evaporation in peatlands which in turn favoured the persistence of the water table at high levels. As we lack reliable pollen and plant-macrofossil data for the most recent centuries, the latter hypothesis would be consistent with (i) the absence of sub-fossil peatland trees during this period at Rieznyčia and numerous other peatlands (Edvardsson et al., 2016b); (ii) the scarcity of tree-ring chronologies extending further back than the early 1800s in studies using living peatland trees (Linderholm et al., 2002; Cedro and Lamentowicz, 2011; Edvardsson and Hansson, 2015; Edvardsson et al., 2015a); (iii) the widespread reestablishment of pine trees observed at the Čepkeliai peatland and in entire Lithuania (Edvardsson et al., 2015b) at the termination of the LIA likely be linked to warmer climatic conditions causing gradually drier peat surfaces.

The increase of secondary anthropogenic indicators, i.e. *Plantago*, *Chenopodium*, *Artemisia*, *Taraxacum* (Veski, 1998), now reveals clear evidence for increasing human activity in the area. Palaeoenvironmental investigations conducted at the regional scale show increasing anthropogenic pressure during the Historical Times (Stancikaitė et al., 2002). Yet, we believe that the remote investigated area could hardly have been intensively exploited.

5. Conclusions and future outlook

In this study, a multiproxy approach coupling pollen records,

plant macrofossils analyses, and tree-ring analysis of subfossil trees has been used at two peatland sites in southeast Lithuania to unravel the environmental history of the wider study area over the Common Era. Our results highlight changes towards moister conditions for the periods 300–500 CE and 950–1850 CE, whereas changes towards warmer and/or dryer conditions have been recorded about 100, 600, and 750 CE, and since the mid-19th century. Despite the rather limited surface of the Baltic countries (175,000 km²), comparison with previous studies conducted in the region by e.g. Stancikaitė et al. (2002), Lamentowicz et al. (2015) or Gaika et al. (2013, 2017), still demonstrates the large complexity of moisture fluctuations and vegetation dynamics at the regional scale during the Common Era. This complexity is related to (i) the position of the Baltic region at the transitional margin between the temperate and boreal vegetation zones, as well as between the continental climate of the Eurasian mainland and the more oceanic climate of Western Europe (BACC Author Team, 2014); (ii) the high spatio-temporal variability of precipitations (iii) potential interferences between local and more regional evolutions as well as anthropogenic and climatic signals in paleoenvironmental proxies. In this context, our results do not only contribute to a better knowledge about hydroclimatic variability in the Baltics during the Late-Holocene, but also underline the need for further highly-resolved long-term palaeohydrological and botanical records for this region. In a broader context, the development of such records is of prime importance as it will allow a better understanding of vegetation and peatland responses to future climate changes.

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